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La dentition de *Equus lambei* du Pléistocène supérieur provenant des grottes du Poisson Bleu (Yukon) et sa comparaison avec celle des chevaux eurasiens

Zahncharakteristika von *Equus lambei* im späten Pleistozän von den Bluefish-Grotten, Yukon-Gebiet, und ihr Vergleich mit eurasischen Pferden

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Résumé de l'article

Les grottes du Poisson Bleu présentent les témoins les plus anciens découverts in situ d'une occupation humaine en Bérिंगie orientale, associés à la faune la plus nombreuse et diversifiée trouvée dans la région. On présente ici les données issues de l'étude d'un important échantillon de dents de cheval récupérées dans les trois grottes. Cette recherche contribue à enrichir nos connaissances sur *Equus lambei*. La comparaison de la dentition de *Equus lambei* avec celle des chevaux contemporains d'Europe montre que leur dents sont de taille similaire. À la faveur de cette comparaison l'hypothèse d'une réduction de la taille des équidés survenue au Pléistocène supérieur est envisagée.

DENTAL CHARACTERISTICS OF LATE PLEISTOCENE *EQUUS LAMBEI* FROM THE BLUEFISH CAVES, YUKON TERRITORY, AND THEIR COMPARISON WITH EURASIAN HORSES

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ABSTRACT *Dental characteristics of Late Pleistocene Equus lambei from the Bluefish Caves, Yukon Territory, and their comparison with Eurasian horses.* Bluefish Caves I, II and III of northern Yukon, have yielded the earliest *in situ* evidence of human occupation of Eastern Beringia, associated with one of the largest and most diverse Late Pleistocene faunas recovered in the region. This paper presents data derived from the study of a large sample of horse teeth recovered from the three caves. This research contributes to our knowledge of the Late Pleistocene Beringian equid, *Equus lambei*. A comparison of the dentition of *E. lambei* with that of some contemporary European horses, indicates they have similar size cheekteeth. The hypothesis of a Late Pleistocene trend of size reduction in equids is considered in the light of this comparison.

RÉSUMÉ *La dentition de Equus lambei du Pléistocène supérieur provenant des grottes du Poisson Bleu (Yukon) et sa comparaison avec celle des chevaux eurasien.* Les grottes du Poisson Bleu présentent les témoins les plus anciens découverts *in situ* d'une occupation humaine en Béringie orientale, associés à la faune la plus nombreuse et diversifiée trouvée dans la région. On présente ici les données issues de l'étude d'un important échantillon de dents de cheval récupérées dans les trois grottes. Cette recherche contribue à enrichir nos connaissances sur *Equus lambei*. La comparaison de la dentition de *Equus lambei* avec celle des chevaux contemporains d'Europe montre que leur dents sont de taille similaire. À la faveur de cette comparaison l'hypothèse d'une réduction de la taille des équidés survenue au Pléistocène supérieur est envisagée.

ZUSAMMENFASSUNG *Zahncharakteristika von Equus lambei im späten Pleistozän von den Bluefish-Grotten, Yukon-Gebiet, und ihr Vergleich mit eurasischen Pferden.* Die Bluefish-Grotten I, II und III von Nord-Yukon haben den frühesten Beleg *in situ* über menschliche Besiedlung von Ost-Bering erbracht, in Verbindung mit einer der bedeutendsten und abwechslungsreichsten Fauna des späten Pleistozäns, die man in diesem Gebiet finden konnte. Dieser Aufsatz stellt Daten vor, die bei der Studie einer bedeutenden Sammlung von Pferdebackenzähnen aus den drei Grotten gewonnen wurden. Diese Forschungsarbeit bereichert unsere Kenntnisse über *Equus lambei* im späten Pleistozän. Ein Vergleich der Dentition von *E. lambei* mit der einiger zeitgenössischer europäischer Pferde zeigt, daß ihre Backenzähne fast gleicher Größe sind. Die Hypothese, daß im späten Pleistozän ein Trend zum Kleinerwerden der Pferde bestand, wird im Licht dieses Vergleichs in Erwägung gezogen.

INTRODUCTION

The paleoenvironmental record for eastern Beringia is preserved virtually intact in many deposits in the northern Yukon, Northwest Territories and Alaska. These deposits yield an almost continuous record of environmental conditions during the last glacial period, or Wisconsin (Hughes *et al.*, 1981; Harington, 1978; Morlan, 1980). They have been the focus of several multi-disciplinary projects, such as the Northern Yukon Research Programme (Irving *et al.*, 1989), the Yukon Refugium Project (Hughes *et al.*, 1981) and an ongoing, long-term study of Pleistocene vertebrate fossils undertaken by the Canadian Museum of Nature (Harington, 1989).

Unglaciated lowland areas in eastern Beringia, including the Bonnet Plume, Old Crow, Bluefish and Bell basins, may have played a part in the peopling of the New World,

particularly during the maximum expansion of the Cordilleran and Laurentide ice sheets. For this reason archaeologists seek a better understanding of Late Pleistocene environments in this region.

The floral and faunal communities of eastern Beringia, though still poorly known, appear to have differed fundamentally from present tundra communities (Harington, 1977; Guthrie, 1982, 1985a; Matthews, 1982; *inter alii*). The Mammoth Fauna, a widespread faunal community during the Late Pleistocene in Beringia, was dominated by mammoth, horse and bison (Guthrie, 1982, 1985a; Matthews, 1982; Vereshchagin and Baryshnikov, 1982), and only loosely associated with elements such as *Saiga* and *Ovibos*. At Bluefish Caves (Fig. 1), however, elements of the Mammoth Fauna are closely associated with both *Saiga* and *Ovibos*. A better un-

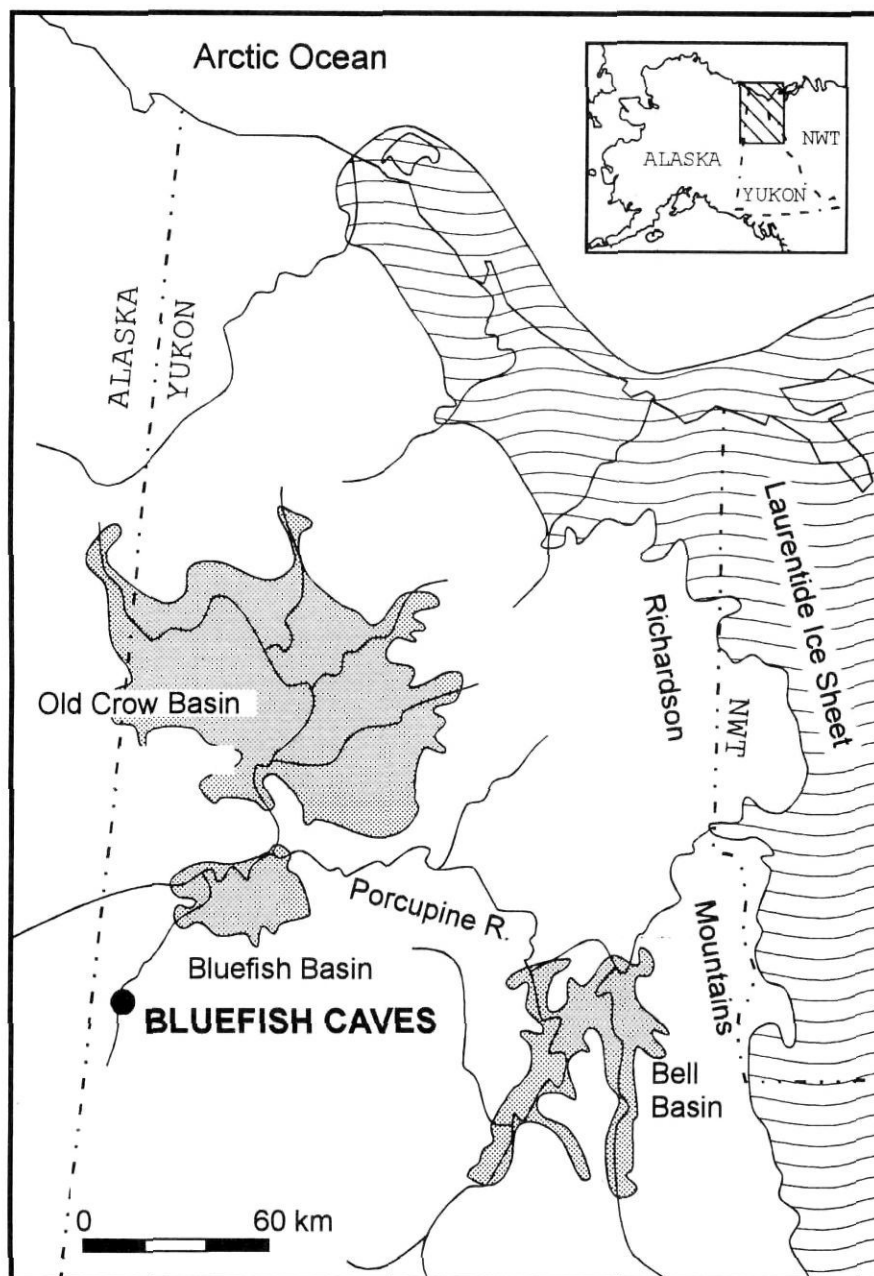


FIGURE 1. Map showing the location of the Bluefish Caves relative to the distribution of the northern Yukon-eastern Beringian, Late Pleistocene glacial lake basins and the northernmost boundaries of the Late Wisconsin Laurentide Ice Sheet.

Carte de localisation des grottes du Poisson Bleu (nord du Yukon) en relation avec la répartition des lacs glaciaires au Pléistocène supérieur et des marges septentrionales de l'Inlandsis laurentidien du Wisconsin supérieur.

derstanding of Late Pleistocene faunal communities in eastern Beringia has been hampered by the lack of *in situ*, identifiable biocenoses (Matthews, 1982; Guthrie, 1985a).

The presence of *in situ* palynological remains, and abundant faunal remains in the three Bluefish Caves, make this an invaluable assemblage for furthering our knowledge of animal communities and their environment in eastern Beringia.

HORSE REMAINS FROM THE BLUEFISH CAVES

Horse remains have been discovered at Bluefish Caves in stratigraphic contexts spanning the last 15,000 years of the Late Pleistocene (Cinq-Mars, 1990). These fossils help clarify the relationship between the behaviour and morphology of Beringian equids, and paleoenvironmental conditions during the Late Pleistocene.

At Bluefish Caves, teeth are numerous and well-preserved. Furthermore, teeth, and third metacarpals, have proven useful as a basis for taxonomic determinations of Pleistocene fossil horses (Prat, 1976, 1980; Eisenmann, 1980, 1986, 1991; Azzaroli, 1990). Dental measurements have also been used as a measure of overall body size in Pleistocene equids (supra, and see MacFadden, 1992: 269). Here, we describe the dentition of *Equus lambei* for purposes of taxonomic comparison with the Pleistocene equids of Europe. Postcranial remains of *Equus lambei* from Bluefish Caves are currently under study (C.R. Harington, Canadian Museum of Nature).

The possibility of detecting trends in the body-size of Eurasian Late Pleistocene equids is controversial (Forstén, 1991; Eisenmann, 1991). The correlation between trends in equid body-size and Pleistocene climatic phases is not well established (Forstén, 1993), although its potential evolutionary significance has been recognized (Forstén, 1991, 1993; Eisenmann, 1991). We help to clarify relationships between equid body size and climate by giving the tooth measurements of a local population, or deme, of horses, from a well-defined Late Pleistocene environment.

DATING OF *E. lambei* REMAINS IN EASTERN BERINGIA

Equus lambei, the horse represented in the Bluefish fauna, is characteristic of Wisconsinan faunas in the steppe-like terrain of eastern Beringia (Harington and Clulow, 1973; Harington, 1978:84, 1980). *E. lambei* appears in pre-Late Wisconsinan deposits in Dawson, Old Crow and Alaska, and in Illinoian age deposits in Alaska (Hughes *et al.*, 1981). At Bluefish, *Equus lambei* specimens have been radiocarbon dated between: $12,900 \pm 100$ BP (GSC 28881, *E. lambei* femur, cave I) and $17,440 \pm 220$ BP (RDDL 278, *E. lambei* metatarsal, cave I). Two additional bone fragments, identified as equid, have been dated to $12,290 \pm 440$ (NMC 1236, cave III) and $22,680 \pm 530$ (NMC 1237, cave II) respectively.

A relatively small, broad-skulled horse, *Equus lambei* strongly resembles Late Pleistocene equids from Siberia (Harington, 1974: 647; Eisenmann, 1986: 72). The type specimen, from Gold Run Creek, Alaska, was first described by Hay in 1917.

Equus lambei has been variously described as a member of the genus *Asinus* (Groves and Mazak, 1967; Harington, 1977), as a caballine (Savage, 1951, as quoted in Harington, 1977: 630; Groves 1974) and as an onager (Quinn 1957, as quoted in Harington 1977: 630). *E. lambei* is now firmly assigned to the caballine group on the basis of physical traits described by Harington (1980) and Forstén (1986), and multivariate analyses carried out by (Eisenmann, 1980, 1986). Eisenmann noted close similarities between *Equus lambei*, Late Pleistocene European and Siberian horses, and modern ponies. Similarly, Forstén (1988a:163) states that *E. lambei*, the Yukon horse, was "the easternmost

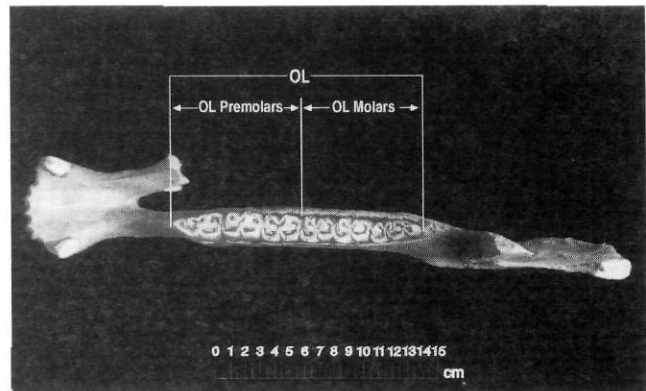


FIGURE 2. *E. lambei* mandible, Bluefish Caves (Cave III). OL stands for occlusal length, measured including the band of coronal cementum (OLE is measured on the enamel only).

Mandibule de *E. lambei*, grottes du Poisson Bleu (grotte III). OL indique la longueur occlusale incluant le cément (OLE est mesuré à partir de l'émail).

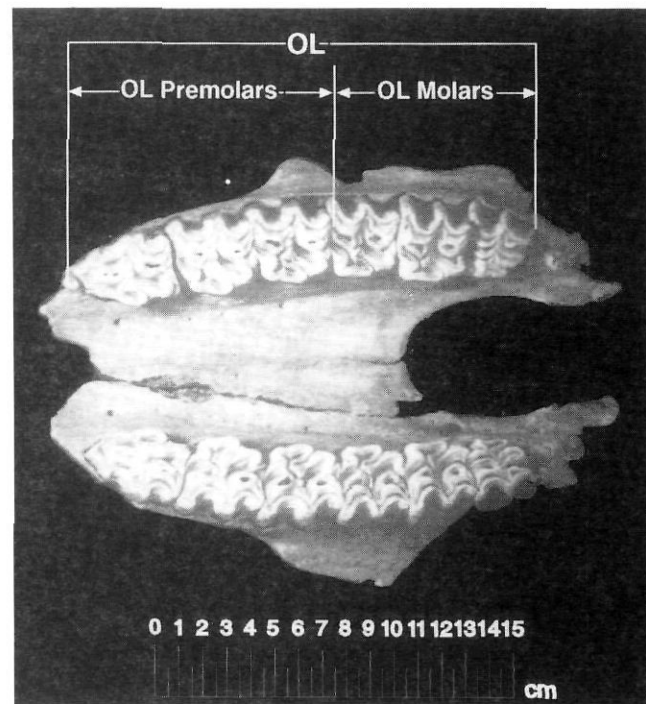


FIGURE 3. *E. lambei* maxilla, Bluefish Caves (Cave III).

Maxillaire de *E. lambei*, grottes du Poisson Bleu (grotte III).

representative of a circumpolar species of small, cabaloid, horse of which Przelwalski's horse and the tarpan were the last wild Eurasian survivors". The inclusion of *E. lambei* into the cabaloid group is now accepted by Harington (1989: 95).

METHODOLOGY

The Bluefish Caves have yielded 524 horse cheekteeth, so far: 306 upper, and 218 lower. (Figs. 2 and 3). The teeth

TABLE I

Qualitative data for *E. lambei*, following Eisenmann (1986)
(upper cheekteeth/complete rows only)

	P3/P4 char.1	M3 char.2	M3 char.3	P1 char.4
T.P.1-F-35 g	5	0	1	?
T.P.1-F-35 d	6	0	0	?
M-9-94 d	6	0	1	?
M-9-94 g	7	0	0	0
85-115 d	5	1	0	0
85-115 g	6	0	0	?
85-62 d	7	?	?	1
85-62 g	7(dP4)	?	?	1
S-3-79 d	8	0	1	0
T.P.1-E-46 d	5	0	1	1
T.P.1-E-46 g	6	0	1	0
M-9-111+112d	7	0	0	0
M-9-111+112g	6	0	0	0
T.P.1-E-61	5	0	0	?
85-120	5	1	0	?
E3-4-3	7	0	0	?
85-MISC-2.1	5-6	0	0	0
G7(E1/2)-9-1	4	0	1	?
TOTALS (N=18)	6%	11%	33.3%	16%

Char.1 - # folds on P3/P4. Char.2 - isolated hypoglyphs on M3.

Char.3 - open post-fossettes on M3. Char.4 - presence dP1 on adult specimen.

Adjusted totals: with the addition of isolated M3s :

	Char.1	Char.2	Char.3	Char.4
Bluefish Average Values	6 (N=18)	10.3% (N=29)	34.5% (N=29)	16.0% (N=18)

Isolated M3s :

M3	char.2	char.3
H7(E)-20-5	0	0
H7(E0-16-9	0	0
G7(E1/2)-11-11	0	0
J8-1-138	1	1
K7-5-20	1	1
I7-1-56	0	1
E6-4-55	0	0
S-3-9	0	0
85-MISC-34	0	0
85-MISC-132	0	1
85-41	0	0
TOTALS (N=11)	36.4%	9%

were sorted by anatomical position where possible, and the total number of teeth for each position was calculated. The dental MNI (Minimum Number of Individuals) based on cheek teeth is 51 (25 individuals from Cave I, 13 from Cave II and 13 from Cave III).

Mandibular cheekteeth were measured on seven dimensions, maxillary teeth on five dimensions. Measurements were taken following Turnbull (1986), at the occlusal surface for ease of comparison with Eisenmann's (1980) morphometric data. Prat (1968) suggests measuring 2 cm from the base, or fork, of the roots, in an attempt to control for the reduction in total occlusal surface area which occurs with age. Eisenmann (1980: 81), however, notes that this technique does not improve accuracy since teeth at similar heights are sometimes not at the same wear stage; furthermore, it makes some measurements (e.g. protocone length) more difficult. Measuring near the tooth root also necessitates the removal of teeth from the jaw in cases where tooth rows are intact. A series of qualitative observations were also made on the upper cheekteeth following Eisenmann (1986: fig. 19).

The quantitative data are used to confirm the taxonomic affiliation of *E. lambei*, to describe the dental characteristics of *E. lambei* more fully than before, and to compare *E. lambei* with various Eurasian horses measured by Eisenmann (1980, 1986). Upper cheekteeth are preferred over lower cheekteeth or incisors in these comparisons, as they are the tooth category which has received the fullest treatment in the literature (e.g., Levine, 1982; Turnbull, 1986; Zeder, 1986; Eisenmann, 1990; Forstén, 1990, 1991). Finally, incisors are notoriously difficult to identify as to anatomical position once they are loose, and are frequently under-represented in archaeological assemblages.

RESULTS

Qualitative dental characteristics of *E. lambei* (Table I) are only roughly similar to those of *E. przewalskii*, the only living representative of the wild horse (for full description of these characteristics, see Eisenmann, 1986: fig.19). The average number of enamel folds on P3 and P4 is higher in our sample of *E. lambei* (6 rather than 4-5), the frequency of isolated

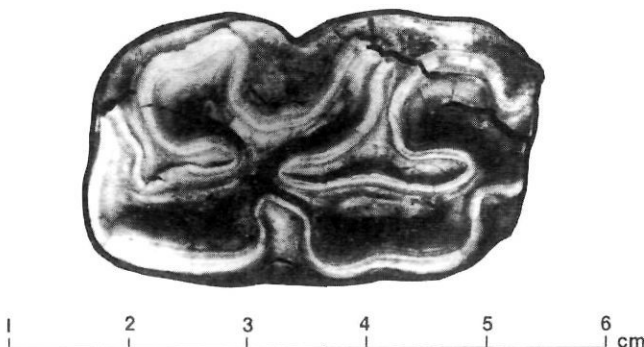


FIGURE 4. *E. lambei*: occlusal surface of lower cheektooth showing a typically cabaloid entoflexid pattern.

Surface occlusive d'une dent jugale inférieure de *E. lambei*: exemple typique.

hypoglyphs on M³ is much less (10.3% rather than 47%), the frequency of open post-fosettes on M³ is higher (34.5% rather than 27%) and the frequency of dP¹ in adult specimens less (16% instead of 25%). These differences can probably be attributed to genetic differences between local populations — or rather between the local population of *E. lambei*, at Bluefish, and the average values for *E. przewalskii* as sampled by Eisenmann. The variation in these qualitative characteristics for the two caballine groups observed here suggests that

they may prove useful in distinguishing between caballine subspecies.

One further qualitative characteristic is observed: there is a basic difference in the shape of the entoflexid in lower teeth, between "U" pattern cabaloids, which include *E. caballus* L., and "V" pattern stenonids, which include fossil stenonid horses (*Equus stenonis* Cocchi), *E. zebra* L., *E. greyi* Oust., *E. burchelli* (Gray), *E. asinus* L., *E. hemionus* Pallas and *E. kiang*

TABLE II
Morphometric data for lower cheekteeth of *E. lambei*, Bluefish Caves

		n	Mean values	Minimum	Maximum	S	V
P2	OL	34	31.87	24.61	35.98	2.332	5.438
	AW	34	12.47	10.49	14.79	0.969	0.939
	PW	34	14.51	11.74	15.93	0.997	0.994
	L	34	15.28	11.58	19.237	1.474	2.174
	W(v)	34	7.01	1.74	9.89	1.460	2.150
	Lpf	34	15.51	4.50	18.84	1.863	3.474
P3/4	OL	3	27.96	25.51	30.64	2.572	6.617
	AW	3	16.62	15.41	18.34	1.530	2.343
	PW	3	16.86	15.31	17.75	1.351	1.827
	L	3	17.14	16.35	17.678	0.703	0.495
	W(v)	3	5.72	3.77	8.23	2.281	5.203
	Lpf	3	13.89	11.36	16.56	2.602	6.774
M3	OL	30	30.04	23.89	33.60	2.580	6.659
	AW	30	13.39	10.32	15.71	1.186	1.408
	PW	29	12.26	10.24	13.86	0.979	0.958
	L	30	12.98	11.09	14.312	0.907	0.822
	W(v)	30	3.43	0.79	5.29	1.508	2.274
	Lpf	30	11.13	8.13	12.76	1.216	1.480
P3	OL	34	28.58	26.22	30.99	1.803	3.253
	AW	34	15.69	12.60	18.09	1.167	1.364
	PW	34	16.53	15.06	18.55	1.049	1.101
	L	34	16.37	14.81	17.696	0.834	0.696
	W(v)	34	5.96	4.12	8.87	1.024	1.050
	Lpf	34	14.54	11.77	16.45	1.163	1.353
P4	OL	33	27.62	22.63	30.11	1.689	2.853
	AW	33	15.86	9.88	18.96	1.737	3.020
	PW	33	16.20	11.88	18.03	1.415	2.0
	L	33	15.30	12.29	16.997	1.169	1.368
	W(v)	33	5.13	3.02	7.83	1.060	1.125
	Lpf	33	12.70	5.38	16.61	2.179	4.749
M1	OL	29	26.12	20.21	34.80	2.923	8.547
	AW	29	15.06	9.99	16.64	1.233	1.521
	PW	29	14.24	11.02	16.06	1.096	1.202
	L	29	13.75	11.38	14.927	0.881	0.777
	W(v)	29	2.74	1.32	5.91	1.212	1.469
	Lpf	29	10.26	5.92	13.25	2.025	4.102
M2	OL	28	26.70	22.48	32.35	2.278	5.190
	AW	28	14.66	13.00	15.79	0.847	0.717
	PW	28	14.04	11.26	16.54	1.126	1.268
	L	28	13.71	12.22	14.688	1.205	1.452
	W(v)	28	2.77	1.00	7.73	1.456	2.120
	Lpf	28	10.50	3.13	13.04	2.444	5.974

Measurements are given in mm.s

Moorcr. (e.g., Eisenmann, 1981: Figs. 3, 4, 5; Forstén 1988b: 24). The Bluefish horses show a typically caballoid, "U" shaped entoflexid (Fig. 4).

Morphometric data from the present sample (Tables II and III) are graphically compared with mean values for *E. przewalskii*, *E. caballus*, *E. kiang*, *E. hemionus*, and *E. asinus* (Figs. 5, 6, 7 and 8). These data confirm that *E. lambei* resembles another Pleistocene caballoid, (viz., *E. Przewalskii*), rather than the stenorid group (of which *E. kiang*, *E. hemionus*, and *E. asinus* are part).

Eisenmann (1980) attributes taxonomic importance to the *Index Protoconique* (IP), defined as the ratio between the length of the protocone and the occlusal length of the tooth (Eisenmann, 1980: 82). IP values calculated here for *E. lambei* are slightly higher than the values calculated by Eisenmann (1980) for *E. przewalskii*, the wild horse (Fig. 7). The same relationship prevails between IP values within the tooth row, however. The higher IP values for *E. lambei* are a function of the longer protocone lengths (PL) for this subspecies, and the smaller mean occlusal lengths of the teeth (OL).

TABLE III
Morphometric data for upper cheekteeth of *E. lambei*, Bluefish Caves

			n	Mean	Minimum	Maximum	S	V
P2	OLc	OLe	27	36.148	29.944	39.113	2.145	4.603
	LP	OW	37	37.069	29.06	40.274	2.564	6.578
	IP		38	9.377	7.01	16.23	1.690	2.859
			38	24.336	20.170	27.731	1.739	3.024
			27	25.221	20.934	29.856	2.190	4.798
P3/P4	OLc	OLe	2	26.878	26.697	27.058		
	LP	OW	2	26.907	26.907	27.124		
	IP		2	15.321	14.117	16.525		
			2	28.109	28.109	28.384		
			2	56.976	56.976	61.073		
M1/M2	OLc	OLe	3	24.599	23.309	25.725	1.216	1.479
	LP	OW	3	25.382	23.368	27.924	2.323	5.398
	IP		3	13.511	12.725	14.160	0.727	0.529
			3	25.424	25.039	25.737	0.354	0.125
			3	54.919	54.593	55.121	0.285	0.081
M3	OLc	OLe	19	27.271	25.11	29.949	1.155	1.335
	LP	OW	27	27.309	20.58	32.760	2.415	5.836
	IP		29	14.877	12.680	18.08	1.247	1.555
			28	22.321	18.32	24.198	1.338	1.792
			19	55.554	49.164	62.169	3.117	9.718
P3	OLc	OLe	27	28.814	23.723	36.906	2.632	6.931
	LP	OW	40	28.760	22.539	38.948	2.766	7.655
	IP		41	13.813	8.2	17.134	2.031	4.125
			40	26.530	21.518	29.86	1.966	3.867
			26	50.164	41.867	62.363	5.578	31.11
P4	OLc	OLe	23	27.593	22.418	30.24	1.966	3.865
	LP	OW	37	27.836	21.897	31.72	1.946	3.789
	IP		38	14.207	10.47	16.428	1.657	2.748
			38	26.527	22.31	29.00	2.603	6.776
			22	51.601	39.192	58.428	4.390	19.27
M1	OLc	OLe	41	25.355	20.761	35.633	2.453	6.019
	LP	OW	53	25.342	19.337	36.850	2.843	8.087
	IP		53	13.775	9.49	16.433	1.591	2.531
			52	25.660	17.95	28.52	2.575	6.632
			39	54.930	44.76	65.184	4.339	18.82
M2	OLc	OLe	32	25.798	21.854	29.54	1.611	2.597
	LP	OW	46	26.102	21.97	33.76	1.940	3.765
	IP		46	14.548	12.44	17.299	1.110	1.233
			46	24.806	19.90	26.992	1.378	1.901
			31	56.556	47.158	62.868	3.658	13.38

Measurements are given in mm.s

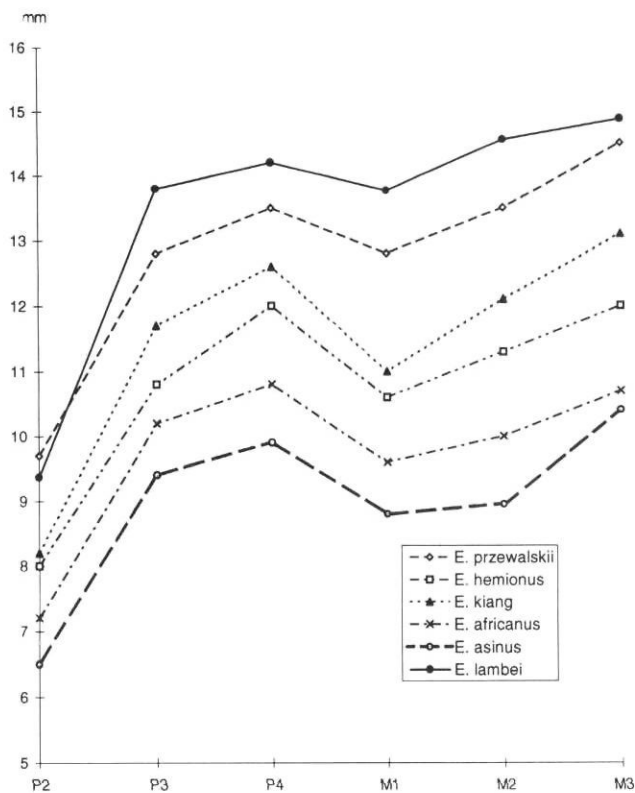


FIGURE 5. Mean protocone length of various equids: upper cheekteeth. After Eisenmann (1986).

Longueur moyenne du protocône chez diverses espèces d'équidés: dents supérieures (selon Eisenmann, 1986).

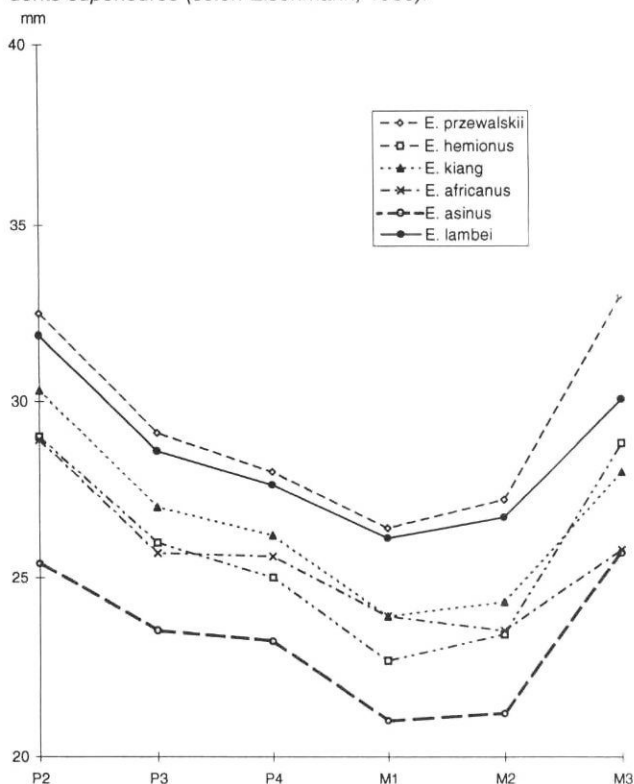


FIGURE 7. Mean occlusal length for the lower cheekteeth of various equids. After Eisenmann (1986).

Longueur occlusive moyenne, dents inférieures chez diverses espèces d'équidés (selon Eisenmann, 1986).

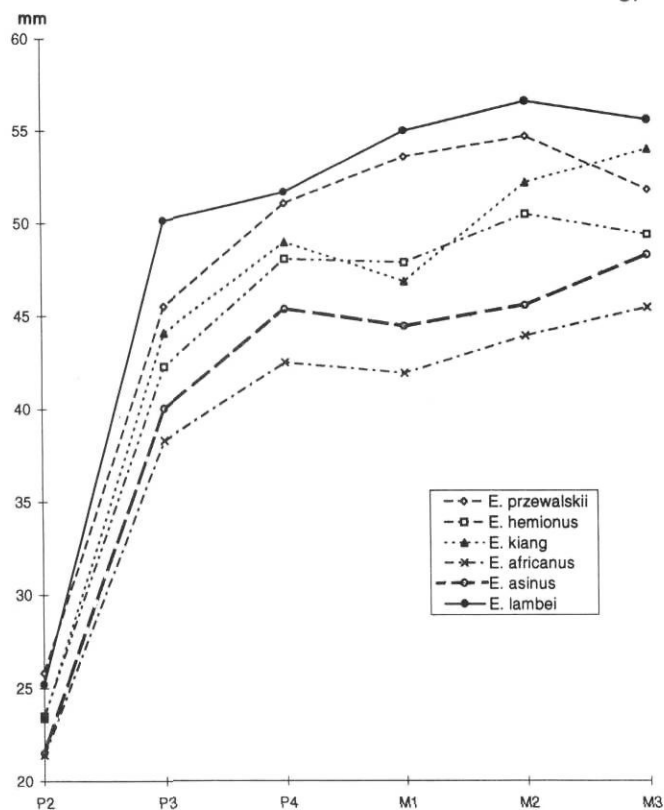


FIGURE 6. Mean protocone indices for various equids: upper cheekteeth. After Eisenmann (1986).

Indices moyens du protocône chez diverses espèces d'équidés: dents supérieures (selon Eisenmann, 1986).

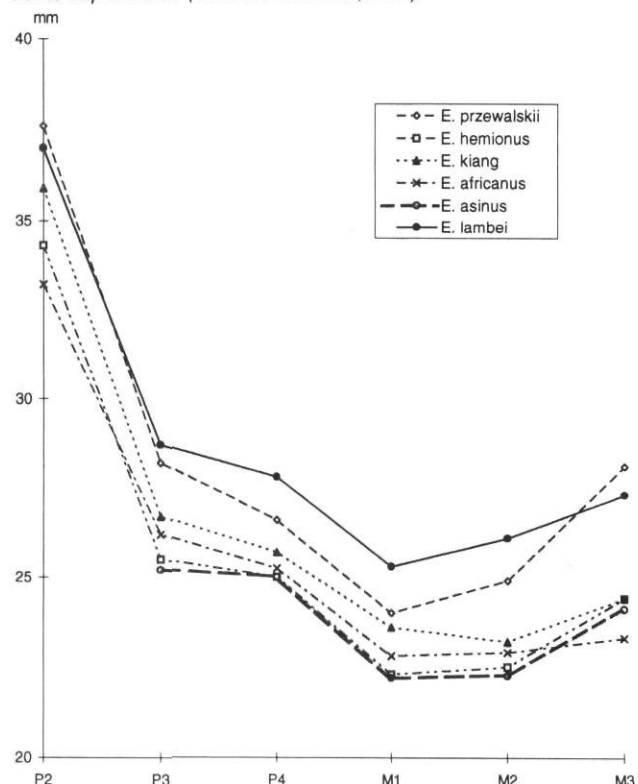


FIGURE 8. Mean occlusal length for the upper cheekteeth of various equids. After Eisenmann (1986).

Longueur occlusive moyenne, dents supérieures chez diverses espèces d'équidés (selon Eisenmann, 1986).

TABLE IV
*Cranial measurements of E. lambei: overall length of the tooth rows,
 premolar and molar rows*

Upper cheekteeth (see Figure 5 for measurements taken) :

N=19	OL (mm) Cheekteeth	OL Premolars	OL Molars	Notes
1.	172.58	94.88	79.24	
2.	173.52	95.11	78.85	
3.	167.28	92.18	76.51	
4.			78.14	missing M
5.	172.66	95.02	79.43	
6.			78.56	
7.		(92.90)		deciduous
8.		(92.65)		deciduous
9.	164.72	96.02	72.14	
10.	(180.53)	(102.58)		(incl. dP1)
11.	175.02	98.91	77.89	
12.	170.25	95.18	75.78	
13.	167.72	92.12	76.86	
14.	168.35	92.44	76.02	
15.	162.47	92.31	70.33	
16.	167.96	90.65	76.52	
17.	168.83	93.11	75.97	
18.		90.83		PMs only
19.	167.11	92.98	missing M1	senescent
Average values	(N=13) 168.80	(N=14) 93.69	(N=14) 76.59	

Tooth row lengths: Lower cheekteeth (see Figure 7 for measurements taken) :

N=17	OL (mm) Cheekteeth	OL Premolars	OL Molars	Notes
1.	170.22	87.08	82.43	
2.	168.55	95.10	76.78	M3 erupting
3.		92.11		M3 absent
4.	166.48	86.08	80.61	
5.	163.57	85.51	79.56	senescent
6.	171.41	93.69	77.80	M3 just worn
7.	166.26	88.64	76.84	
8.	176.29	92.24	82.25	
9.	165.36	87.52	78.95	
10.	166.76	87.63	80.69	
11.			80.57	missing PM
12.	166.32	86.79	80.69	
13.	169.50	88.96	80.85	
14.			74.72	missing P2
15.	167.96	84.70	79.70	large (PM) interstices
16.	168.30	87.08	79.94	
17.	170.92	87.76	81.70	
Average values	(N=14) 168.42	(N=15) 88.73	(N=16) 79.6	

Measurements given in mm.s.

The presence of relatively long protocones is considered by Eisenmann (1980: 105) to be characteristic of modern horses in general and *E. przewalskii* in particular. It is interesting that *E. caballus* from Liakhov Islands, a small, Siberian contemporary of *E. lambei*, has relatively high IP values (Eisenmann, 1980: 125), especially on the molars. The similarity between this equid and *E. lambei* is therefore noted here. It should also be noted that Forstén (1982) considers the protocone index (ff. Eisenmann, 1980, 1986) invalid for taxonomic characterisations because of: 1) size differences observable within the same subspecies of horse; and 2) allometric associations between the recorded dimensions and overall body size. The authors tend to agree with Forstén with regards to the taxonomic usefulness of the IP. We are primarily interested in its potential allometric use.

Further quantitative measurements presented here (Table IV) include overall length of the tooth row (OL), and length of the molar and premolar rows. Measurements were taken following Von den Driesch (1976) and are illustrated in Figures 2 and 3.

CANINE TEETH

The skeletons of modern horses are virtually the same except for the presence of canine teeth in males and relatively smaller or absent canines in females (Berger, 1986: 21). This means that canine teeth are one of the few qualitative characteristics which may be used to reconstruct socioeconomic ratios in fossil populations (MacFadden, 1992: 272-273). MacFadden (1992: 273) states that: "With sufficiently large and well-preserved samples, canine dimorphism is seen to have been common in virtually all extinct horses".

Many horses in the Bluefish fauna have large, well-developed canines¹ (Fig. 9). In Cave I, only one adult anterior jaw is present and it contains a well-developed canine. In Cave II, 3 of 5 adult anterior jaws contain well-developed canines. In Cave III, 11 out of 14 anterior jaws (of which 2 are immature) contain canines, i.e. 11 out of 12 adult anterior jaws have well-developed canine teeth (Table V). Several possibilities are raised by these data: 1) a succession of small bachelor bands came to grief near the caves; 2) selective predation upon adult males was taking place; 3) retention of canines in females is a characteristic of *E. lambei*, in which case the presence of canine teeth cannot be used to infer sex ratios for this subspecies.

Horse herds live either in family bands composed of an adult male, and females with their foals, or in bachelor bands: small, unstable groups of fewer than four young males (Waring, 1983: 142). In Caves II and III yearlings are present in the death assemblage, which points to the presence of some family bands rather than only bachelor bands - weakening the case for option 1. A pattern of selective predation of adult male horses at Bluefish (option 2) is unexpected, given the large number of different-sized predators active in the vicinity of the caves (Cinq-Mars, 1990). Of the three options, therefore, option 3 seems a plausible explanation of

1. The canine teeth were not measured, as this would have necessitated removal from the jaws.

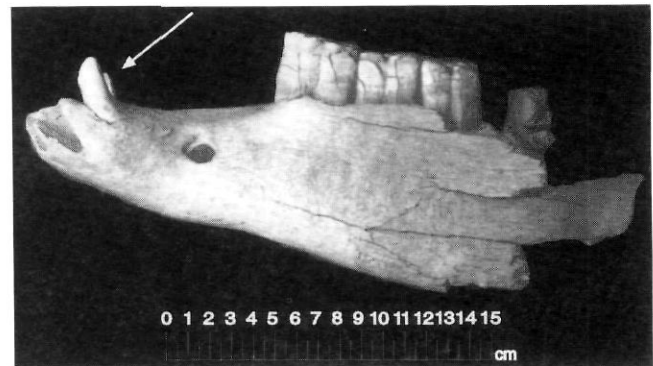


FIGURE 9. Mandible of *E. lambei* (Bluefish Caves) showing typically well-developed canines, potentially characteristic of the species.

Mandibule de E. lambei (grottes du Poisson Bleu) comprenant des canines bien développées, probablement caractéristiques de l'espèce.

the observed ratio of jaws with and without canine teeth. In which case, canine teeth would be characteristic of both males and females in *E. lambei*. If large canines are characteristic of both sexes in *E. lambei*, as the data suggest, this could indicate the retention of a primitive trait, shared with *E. stenonis* (Prat, 1976: 409).

A brief survey by one of us (Burke), of specimens of *E. lambei* from fossil localities in Yukon and Alaska, held at the Canadian Museum of Nature, indicates a high incidence of canines from other fossil localities.

DISCUSSION: IMPLICATIONS OF THE METRICAL INFORMATION

According to Forstén (1993:71) Late Pleistocene horses in northern environments in North America were smaller than their southern contemporaries. On another scale, the muzzle reduction (and a wide choanae) in *E. lambei*, is attributed by Eisenmann (1986: 72) to an adaptation to cold conditions during the Late Pleistocene.

Guthrie (1985b, as cited in Forstén 1993:70) interpreted size reduction in Late Pleistocene non-ruminants (such as the horse) in northern environments as the result of a shortened growth season, conferring an adaptive disadvantage on the conservative growth strategies of non-ruminants such as horse. Forstén (1993: 71) suggests that body-size reduction in Late Pleistocene caballoids may have had the effect of reducing the gestation period and keeping population size high enough to allow the species to adapt to an unpredictable, glacial environment.

The size/climate association is not perfect. The average body size of *E. conversidens* is about the same as that of *E. lambei* (C.R. Harington, pers. comm., 1995). Furthermore, as in the Late Pleistocene fossil record of Europe, a relatively large subspecies of horse is also found in Late Pleistocene deposits in the Yukon (C.R. Harington pers. comm., 1994). And as Forstén herself (1993:72) points out, size reduction in caballoids set in before the rapid climatic changes at the end of the Late Pleistocene. Previous climatic changes (shifts from glacial to interglacial conditions) occurred during the Middle Pleistocene without affecting equid body-size (supra).

TABLE V
Incidence of canine teeth in *E. lambei* from the Bluefish Cave assemblages

	Cave	U/L	C1	Status
G7(E1/2)-8-1	1	U	Y	well-developed, worn
2-H5-?	2	L	Y	erupting
B3-3-23	2	L	N	
C3(E0-3-19)	2	L	N	
H6-3-14	2	L	Y	vestigial
H6-6-15	2	L	Y	juvenile/alveola present
I5(E)-3-9	2	U	Y	well developed
85-76	3	L	Y	well developed
85-109	3	L	Y	well developed
85-90	3	L	Y	well developed
85-76*	3	L	Y	no tooth/alveola present
S-3-89	3	L	Y	senescent/vestigial
M-9-132	3	L	Y	well developed
T.P.1-D-22	3	L	N	
M-9-136	3	U	Y	alveola present
M-9-97	3	L	N	juvenile
85-95	3	L	Y	well developed
85-81	3	L	Y	erupting
M-9-138a	3	L	Y	well developed
1993 nettoyage	3	U	Y	well developed
85-89	3	L	N	juvenile

Summary :

	Pres.	Abs.	juvenile
Cave 1	1/1	0/1	0/1
Cave 2	3/6	2/6	1/6
Cave 3	11/14	1/14	2/14

N.B. Upper and lower incisor rows only were used in this table (complete and partial)

Perhaps size reduction in northern cabaloids relative to earlier equids in North America, and other Late Pleistocene equids in the south, resulted from rapid environmental change. If so, it seems unreasonable to expect a relative size difference between *E. lambei*, a northern Late Pleistocene equid, and Late Pleistocene equids living in more favourable conditions in Europe.

Tooth size may be used as a measure of body-size in horses, according to some authors (e.g., as suggested in MacFadden, 1992: 269). This simple association is not without criticism, however. For example, Nobis (1971) suggests that modifications in tooth size may not have been synchronous with changes in overall body-size. More frequently therefore, tooth size is used in combination with size of the third metacarpal and phalange (e.g., Forstén, 1990). A comparison of mean tooth sizes is presented here, however, as a preliminary step in assessing body size of *E. lambei* prior to obtaining information on MC-III and phalange size for the Bluefish equids (Harington, in prep.).

Tooth size on two dimensions, overall tooth width (OW) and occlusal length (OLe), for *E. lambei* is compared here with the means from Eisenmann for *E. caballus* and *E.*

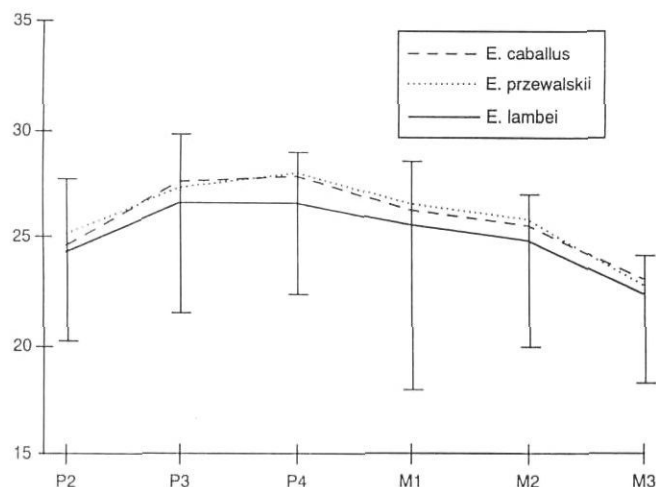


FIGURE 10. Comparison of mean occlusal tooth widths for *E. caballus*, *E. przewalskii*, and *E. lambei*.

Comparaison de la largeur moyenne des dents de *E. caballus*, *E. przewalskii* et *E. lambei*.

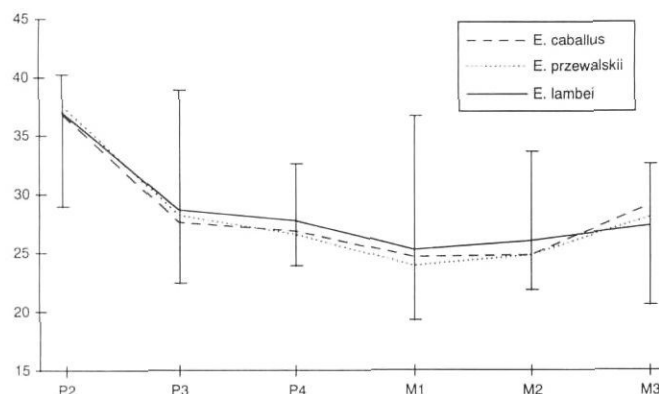


FIGURE 11. Comparison of mean occlusal tooth lengths for *E. caballus*, *E. przewalskii*, and *E. lambei*.

Comparaison de la longueur moyenne des dents de *E. caballus*, *E. przewalskii* et *E. lambei*.

przewalskii (1980; 1986). The comparison indicates that the dentition of *E. lambei* from Bluefish is not smaller than these contemporary European horses. All values for *E. lambei* fall within one standard deviation of Eisenmann's values (Figs. 10 and 11). Mean occlusal lengths (OLe) and tooth widths (OW) of *E. lambei* are lower than the means reported in Eisenmann (1980: Table 46; 1986) for *E. przewalskii* and *E. caballus*, except for occlusal length of P² (Figs. 10 and 11), but fall within one standard deviation of Eisenmann's mean values. The standard deviation for *E. lambei* P² occlusal length overlaps Eisenmann's values.

Forstén (1991: fig. 4), measuring occlusal length, has detected an apparent chronological trend toward tooth size reduction in some local European samples of *Equus*. A comparison of occlusal length (OLe) values for *E. lambei* with the values for mesio-distal length (Levine, 1982: table 1) for Upper Pleistocene fossil populations of Western European horses, shows that the Bluefish population is not significantly

TABLE VI

A comparison of size differences estimated occlusal length (OLe) between *E. lambei* and European Upper Pleistocene horses reported in Levine (1982: 232).

Tooth element	Height (mm)	Mean OLe <i>E. lambei</i> (mm)	Standard deviation <i>E. lambei</i>	N <i>E. lambei</i> sample	N Levine sample	Mean OLe Levine sample	Z*
P ²	35-40	37.6	1.64	N=5	N=14	37.4	-0.09
P ³	35-40	29.8	4.32	N=6	N=9	29.9	0.02
	45-50	27.5	NS*	N=2	N=17	30.2	NS
	65-70	29.4	NS	N=2	N=10	31.4	NS
P ⁴	45-50	25.8	NS	N=1	N=12	28.7	NS
	75-80	28.7	NS	N=1	N=10	29.8	NS
M ¹	35-40	24.0	0.99	N=6	N=7	25.8	1.82
	40-45	24.2	NS	N=3	N=16	25.7	NS
	65-70	25.6	0.69	N=5	N=16	27.4	2.61
	70-75	26.8	0.65	N=3	N=5	28.3	NS
M ²	45-50	24.6	NS	N=1	N=5	27.7	NS
	70-75	26.1	0.12	N=3	N=9	26.9	NS
	75-80	26.8	0.47	N=4	N=3	28.4	3.36
M ³	25-30	29.0	NS	N=1	N=5	27.6	NS
	40-45	26.1	NS	N=2	N=1	25.7	NS
P ₂	25-30	32.2	NS	N=2	N=1	30.1	NS
	30-35	34.2	NS	N=1	N=5	31.1	NS
	45-50	32.8	2.26	N=5	N=9	31.7	-0.49
	50-55	33.2	NS	N=2	N=3	31.8	NS
P ₃	30-35	27.7	NS	N=3	N=1	25.0	NS
	65-70	28.8	NS	N=3	N=3	29.0	NS
P ⁴	35-40	27.7	NS	N=1	N=5	26.5	NS
	40-45	26.8	NS	N=2	N=1	24.1	NS
	75-80	28.6	NS	N=2	N=9	27.0	NS
M ₁	35-40	24.2	NS	N=2	N=1	23.2	NS
	65-70	26.9	0.73	N=4	N=9	27.0	0.14
M ₂	40-45	24.9	NS	N=2	N=1	23.8	NS
	75-80	30.8	NS	N=2	N=9	27.7	NS
M ₃	35-40	33.6	NS	N=1	N=5	32.0	NS
	45-50	31.06	NS	N=1	N=1	27.9	NS

* NS= insufficient sample size

different from Late Pleistocene, Western European caballoids in four out of seven measurements (Table VI). Levine's (1979, 1982) fossil population comprises 65 "assemblage units", representing either distinct stratigraphic units from within a site, or entire site assemblages where the site was excavated in a single unit (e.g., at Jaurens). Sites sampled by the author (Levine, 1979:120, table 19) include: Jaurens; Solutre; Combe Grenal; Arlay; Gigny; and Roc de Marsal, among others.

Occlusal length (OLe) at specific tooth-height intervals for each anatomical position for *E. lambei* were compared with Levine's fossil sample (ff. Levine, 1982). Of 37 categories recorded by Levine (1982: table 1), only seven could be compared due to insufficient sample sizes. Of these, four produced Z-scores (deviation from the mean in standard deviations) within one standard deviation of the European fossil sample; one was within two standard deviations and two were more than two standard deviations from the European fossil sam-

ple (Table VI). Unfortunately, size trends through time such as detected by Forstén (1991) cannot be confirmed at Bluefish due to the undifferentiated nature of the stratigraphy from about 15,000 BP to the Holocene boundary.

CONCLUSION

We confirm the identification of *E. lambei* as a caballine horse. Tooth dimensions of *E. lambei* also indicate its resemblance to *E. caballus* from the Liakhov Islands, Siberia. This enables us to propose palaeoethological reconstructions for *E. lambei* in areas of archaeological interest such as the Bluefish Caves (Burke and Cinq-Mars, in prep.). Both caballoids and stenonids inhabit steppe-like, or savannah-like regions (Berger, 1986) and are non-selective grazers capable of enduring a wide variety of climatic conditions. The principal differences between the caballines and stenonids today lies in their social organization and migration patterns. Caballoids

form small, stable bands of four to ten individuals, whereas stenonids typically do not. Furthermore, modern stenonids migrate in large herds, whereas few caballoids have been observed to do so.

The high ratio of canine teeth in the Bluefish assemblages is either the result of the sampling of more bachelor herds than family herds, or is a genetic trait (retention of canines in females). If this last is true, it could be a useful trait in discriminating *E. lambei* from other Late Pleistocene horses.

E. lambei is similar in size to Late Pleistocene caballoids from Western Europe, as well as to modern caballoids, based on tooth dimensions. This conclusion remains to be tested using metrical data from the post-cranial material excavated at Bluefish caves, specifically MC-III and phalange size (Harington, work in progress). If it is supported by the post-cranial data, this fact has implications for the possible association of body-size in Late Pleistocene equids with environmental conditions. Climatic conditions in eastern Beringia were arguably more critical for horses at the close of the Pleistocene than conditions in Western Europe, and certainly more severe than in Europe today, and yet body size (as measured by tooth dimensions) in *E. lambei* does not appear to reflect this difference in a significant way. However, environmental conditions cannot be the sole factor regulating body-size in equids, and there is no need to postulate that size trends in equids are a unified phenomenon. That is, equid size reduction may not have occurred to the same extent, or for the same reasons, in North America and in Europe.

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